BRIEFER ARTICLES.

DISGUISES IN BUD ARRANGEMENT.

THE law regarding the general arrangement of buds is very simple, but it is not always easy to make all the phenomena of leaf, branch, and flower arrangement agree with the law. This is especially true in the various forms of inflorescence, because in the floral system there is a decidedly greater tendency of potential buds to develop than in the case of the vegetative system; and as flowers can perform their important duty in a somewhat crowded condition as well as when scattered, while leaves must be scattered, the internode is not an important factor in inflorescence as it is in the leaf bearing stem.

One of the simplest disguises of the origin of an inflorescence is seen in various Vitaceæ, Phytolacca, Enslenia, Gonolobus, etc., where each inflorescence terminates the axis, and the succeeding internode is produced by the highest axillary bud. This new internode differs little in size from the preceding, while the stem bearing the inflorescence remains small and is thus thrust aside by the development of the axillary bud. This results in placing the inflorescence opposite a leaf, where it really, but not apparently, terminates the axis. To strengthen this disguise, a small bud is frequently developed in the axil of the leaf opposite the inflorescence, making it appear that the terminal bud has continued the vegetative axis, in which case the inflorescence could have no normally placed bud from which to develop. The nature of this little bud will be considered later.

A still more complete disguise is found in many of the Solanaceæ, where the leaf, which in the above cases stands directly opposite the inflorescence, is carried up by adnation the whole length of an internode from its normal position, leaving the inflorescence apparently branching from an internode instead of a node (*fig. 1*). This also results in an unusual arrangement at the node above, where there are two leaves at one node but not opposite. By tearing a portion of the bark bearing the misplaced leaf down to the level of the inflorescence, both the node bearing the inflorescence and the one above will appear normal.

Physalis goes still farther in this form of disguise, and were one not familiar with a less disguised form, as *Solanum nigrum*, it would be very difficult to determine the normal arrangement of the parts. The internode, which in Solanum separates the inflorescence from the node below, fails to develop in Physalis, thus leaving a flower at a node to which it does not belong and hence neither axillary nor opposite to any leaf at that node. At the same time the leaf which properly opposes the inflorescence is carried upward, as in Solanum, to the level of the next node. If we conceive a node to be formed between the present nodes and the flower raised to it from the node below, and the leaf lowered to it from the node above, the nodes will all be perfectly normal. If the inflorescence of Solanum is split down to the node below, it will be seen to present precisely the arrangement of the Physalis node, and the irregularities may be very easily removed by cutting the flower from one node, and then the leaf to which that flower belongs from the node above, and so on.

FIG. 1. A portion of stem of *Solanum nigrum*, showing position of the inflorescence and of the leaf belonging to the same node.

Dichotomy is another common peculiarity among the Solanaceæ. This is due to the equal development of the primary axis and an axillary branch, and its nature is often obscured by the leaf of the node below being carried, by adnation, to the point where the stem forks, while the leaf to which the lateral branch of the fork is axillary is carried up in a similar manner to the first node of that branch.

The bract of *Tilia Americana* (*fig. 2*) shows how the removal of a bract from its normal position may serve a very useful purpose. This bract is primarily the homologue of a bud scale, or more remotely of a petiole of a leaf. Its midrib is adnate to the peduncle for half the length of the bract, and being persistent with the fruit serves as an efficient means of seed dispersal. There has been some difference of opinion as to the homology of the bract of Tilia, but a careful examination will suggest very forcibly that the bract is a case of adnation

rather than an outgrowth of the peduncle, that it has a foliar rather than a cauline origin. Further proof that this bract is a leaf organ may be found in the buds (represented in cross section in *fig. 2*). Every bud where an inflorescence does not occur has the first bud scale

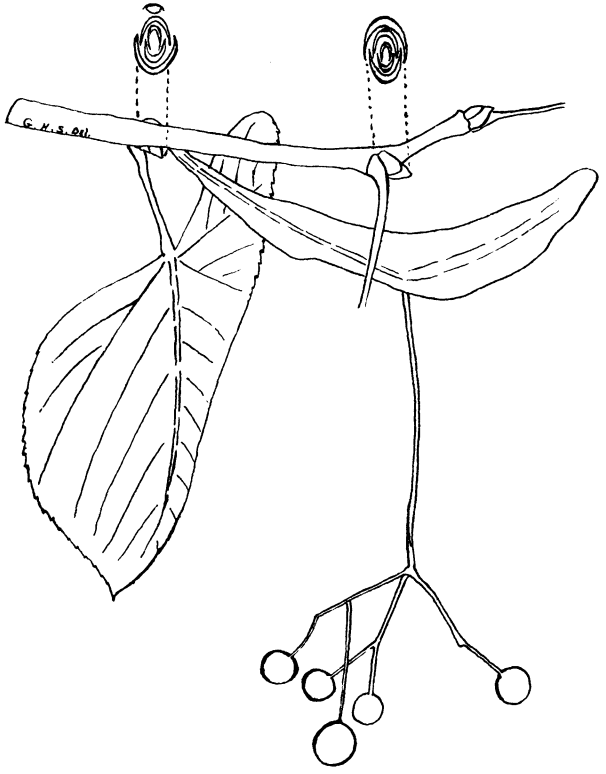

FIG. 2. Infloresence and bract of *Tilia Americana*, with cross section of two buds.

on the upper side. Where an inflorescence appears it always arises from the same position relatively that the first bud scale occupies in other buds, while the bud occurring at the same node with the inflorescence invariably has the first bud scale below.

The removal of a subtending leaf or bract from its normal position is not uncommon. Neither is it always so constant in a species as it seems to be among the Solanaceæ. In a number of species studied the bracts were usually normally placed, but frequently appeared above the node

to which they belonged, or stems were adnate for some distance above the bract, so that the bract appeared to be below the node.

Leaf organs are also frequently absent, but there is always a real or potential bud where the leaf or bract should have been had it been present. Several causes may act to bring about the absence of bracts, but crowding the parts in the bud seems to be the chief cause. The inflorescence of *Sambucus Canadensis* is very interesting in this connection. At the primary division of the inflorescence the five rays are nearly equal, and the four lateral rays are each subtended by a bract which exhibits considerable variation in its position, being frequently above its normal position or below the apparent node. At the secondary, tertiary, etc., divisions of the inflorescence, the parts of the whorl are very unequal, and the larger rays which come in contact with the enveloping leaf organs in the bud, and which thus bear most of the pressure, have the subtending bracts entirely obsolete, while the smaller inner rays from the same nodes, being in the center of the inflorescence, are subjected to less pressure and have minute bracts present.

Without an amendment to the law of bud arrangement a true anomaly occurs in the spikes of *Verbascum Thapsus*. In early development the spike does not appear complex, but in the older spikes or older portions of the spike each bract is seen to subtend a group of buds as shown in *fig. 3*. In the younger portions of the spike the upper bud (1) of the group is the only bud present, and is nestled close in the axil of the bract, hence it is a true axillary bud. This bud is removed from the axil by subsequent growth and another bud (2) takes its place, and is evidently just as truly an axillary bud as the first. About the time this second axillary bud appears, accessories (3, 3) appear at the base of the primary axillary bud, each being subtended by a bract, as is normal with accessory buds. Further growth also removes the secondary axillary bud from the axil of the bract, and a tertiary axillary bud (5) is developed in the axil, while accessories (4, 4) appear at the base of the second axillary bud. I have chosen to call these primary, secondary, and tertiary buds because they in nowise differ from one another except in the time of their appearance.

In a previous paper[1] it was suggested that the bud which produces an extra-axillary branch in the case of *Juglans cinerea* is really the true axillary bud, because no accessory bud was found which regularly pro-

[1] BOTANICAL GAZETTE, **21**: 168. 1896.

duced a branch except in case the axillary bud was destroyed or produced some other organ. Further investigation shows this to be a case precisely similar to that of Verbascum, and the extra-axillary branch is produced by the primary axillary bud while a secondary bud appears in the axil of the leaf. This also occurs in *Juglans nigra* and species of Carya, though here the primary axillary bud is not so far removed from the axil and the secondary remains quite small. To the same class belong those minute buds which occasionally appear in the axil of a leaf after the primary axillary bud has developed into a branch, as in the above mentioned cases where the terminal bud produces an inflorescence and the vegetative axis is continued by the axillary bud.

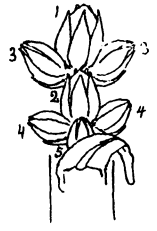

FIG. 3. A group of buds subtended by a single bract in *Verbascum Thapsus*. The numbers indicate the order of development and also of flowering.

There is nothing anomalous about the whorled flower clusters that occur in the axils of the leaves of certain of the Labiatæ, Polygonaceæ, etc., except that the axis of the inflorescence is very much reduced. This is not always plainly evident, but the illustration of *Mentha Canadensis* (*fig. 4*) shows an inflorescence in which this reduction is not complete, and the whole cluster of flowers is plainly seen to be simply a much reduced cyme. Being familiar with such an inflorescence as that of *Mentha Canadensis* it is not difficult to trace the same formation in cases where the reduction is complete and the flowers are sessile. Thus in *Lycopus sinuatus*, for example, the flowers are all sessile, but they may be seen to be divided into two lateral groups with the single flower terminating the central axis.

In Polygonum fascicles of flowers are surrounded at the base by a group of minute scarious bracts, to which the individual flowers are axillary, while in Rumex the flowers are so numerous and so crowded that the bracts are obsolete, but the origin of the flowers is undoubtedly the same as that of the flowers of Polygonum.

The origin and normal arrangement of buds may frequently be inferred from the order of flowering, for anthesis takes place in the order of development. Ordinarily, in a fascicle formed by the reduction of a determinate inflorescence, the flower which blooms first terminates the central axis of the cluster, and the next to bloom will be the terminal buds of the lateral clusters, and so on. In a dense

indeterminate inflorescence the lower or outer buds normally bloom first, because the terminal bud continues vegetative while the axillary buds are forming floral organs. As the order of anthesis and that of development are the same, whatever affects the order of development will in like manner affect the order of flowering. Thus, if for any cause the terminal bud of a normally indeterminate inflorescence develops floral organs before the last lateral buds have attained a like state of development, a mixed inflorescence results, as has been occasionally seen in Digitalis.

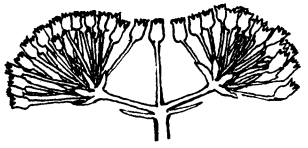

FIG. 4. Verticillate inflorescence of *Mentha Canadensis*.

A very interesting case of variation from the normal order of development is seen in the genus Dipsacus, where the dense crowding of the flowers in the head forces the lower buds down against the involucre and so retards their development. The next circle of buds is not crowded so much, and the development is proportionately less retarded. The pressure becomes less and less as the buds occupy a higher and higher position in the head, until at about the middle a point is reached where the bud pressure is so much reduced that from that point to the apex of the head a normal order of development obtains, showing Dipsacus to have a normally indeterminate inflorescence. In flowering the center of the head blooms first, and thence one flower zone proceeds upward according to the normal order of development, and another downward according to the order of development brought about by bud pressure.

SUMMARY.

1. Most cases of branch and flower arrangement may be explained by the law that a bud, real or potential, occurs in the axil of every leaf, and terminates every axis.

2. If a bud is removed from the axil of a leaf by adnation or by development into a branch, a secondary axillary bud may form in the axil of the leaf, and if that too is removed a tertiary axillary bud may form, etc.

3. Bud pressures explain reduction of bracts and their failure to appear, as well as many modifications in the normal order of anthesis. —GEO. H. SHULL, *Yellow Springs, Ohio.*